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VARIATION IN THE CENTRAL AMERICAN IGUANID LIZARD, *ANOLIS CUPREUS*, WITH THE DESCRIPTION OF A NEW SUBSPECIES

By

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In the course of ecological studies of Costa Rican lizards conducted by the senior author from October 1967 to March 1970, *Anolis cupreus* Hallowell was found in larger numbers and at more localities than any other species of lizard. Approximately 3450 individuals of this small Pacific coast anole were processed and recorded in the field in a mark-and-recapture program. Notable differences were observed between individuals, geographic populations, and the sexes. The recent resurrection of *Anolis hoffmanni* Peters (a species long considered a synonym of *A. cupreus*) by Williams and Smith (1966) together with variation observed among our samples, suggested that more than one taxon was represented in our accumulated field records. In order to determine the number of taxa involved, series of specimens were collected throughout the range of *Anolis cupreus* in Costa Rica and near the northern end of the range of the species in Guatemala. Additional preserved specimens from Costa Rica and western Nicaragua were examined in the University of Kansas Museum of Natural History (KU). Localities represented by our collections are shown in figure 1. Populations of *A. cupreus* at or near all Costa Rican localities shown in figure 1 were studied in all seasons, thereby providing information on population structure and other aspects of natural history.

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The large series of specimens from those localities permitted study of individual variation and sexual differences. Knowledge of such factors enhances the validity of geographic comparisons.

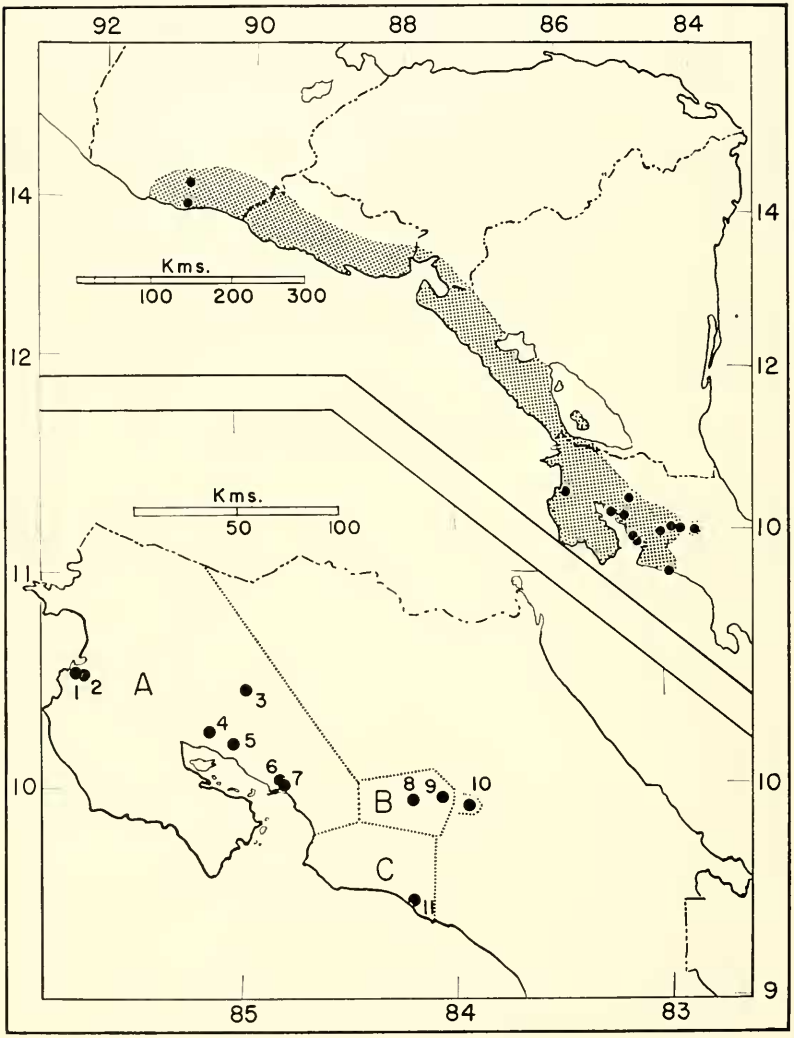

Fig. 1. Map of Central America showing probable range of *Anolis cupreus* (shaded) based on specimens collected by the authors and examined in life (dots), museum specimens, and published records and statements by Taylor (1956), Stuart (1955), and Peters and Donoso-Barros (1970). Inset below is a map of Costa Rica showing probable ranges of three subspecies of *Anolis cupreus:* A. *A. c. cupreus;* B. *A. c. hoffmanni;* C. *A. c. spilomelas.* The localities from which series were examined are: 1. Playa del Coco, 2. Sardinal, 3. Tilarán, 4. Río Higueron, 5. Río Congo, La Irma, 6. Río Naranjo, 7. Boca de Barranca, 8. Turrúcares, 9. San José, 10. Cartago, 11. Quepos.

MATERIALS AND METHODS

Our field data were gathered on six trips to Costa Rica (2 February to 28 March 1965, 13 October 1967 to 16 July 1968, 10 August to 8 September 1968, 18 January to 13 March and 8 August to 8 September 1969, 29 January to 14 March 1970) and one trip to Guatemala, 15 to 24 February 1971, by H. S. Fitch. A. F. Echelle participated in the 1967-68 field trip, and all three authors made the 1970 and 1971 trips together. Population samples, mostly based on live anoles, examined but not killed or removed, were obtained from Costa Rica as follows: on 13 days in eight different months at Boca de Barranca; on two days in one month at Cartago; on 26 days in nine months at La Irma; on 17 days in nine months at Quepos; on three days in three months at Río Naranjo; on 75 days in 19 months at San José; on 15 days in nine months at Sardinal, and on three days in two months at Turrúcares. The samples from Guatemala were obtained on 17, 18 and 19 February, 1971. The small samples that we used from Tilarán and Taboga are in the Museum of Natural History at the University of Kansas.

Many variable characters were examined. Each character was found to have limitations, and each was used on relatively small but representative series of specimens. The conventional characters used in the classification of anoles are those that can be seen in preserved specimens. However, some characters that we found to be equally useful can be seen only in living or freshly killed anoles.

Color and pattern, especially, were found to be useful for showing differences between geographic populations, between age groups, and between the sexes. Because these differences are obscured in preserved specimens, we recorded them only from live or freshly killed anoles. Snout-vent length was measured to the nearest millimeter, and most of the measurements were taken from live lizards or those that were freshly killed. Live weights of most of the anoles processed in 1970 and 1971 were recorded in the field with Oskar Ludi spring scales, to the nearest hundredth of a gram. Length of tail was also recorded for each anole, with regenerated parts noted separately. Relatively large amounts of data were therefore available for size and tail length, and both were found to show significant differences between populations and between the sexes. For comparison of size between populations, only adults were used. Females of 35 mm snout-vent length often contained uterine eggs or enlarged follicles while those that were smaller rarely contained either, hence females of 35 mm in length or larger were considered adults. Males of 40 mm or longer were considered

adults; those that were smaller were found to be still growing rapidly.

Other characters that were used were based upon preserved specimens. Number of scale rows around the body varied significantly between geographic populations and between the sexes, but recording them was tedious because of the small granular scales, and was inexact because of irregularities in the rows. Therefore the counts were made on relatively small series of museum specimens.

VARIATION WITHIN AND BETWEEN POPULATIONS

Size.—In *A. cupreus,* as in most iguanids, the male attains a larger size than the female (Figs. 2 and 3). In every series examined, the males were somewhat larger in maximum size (Fig. 3). There is little or no weight difference between males and females of comparable size. Because of continued growth after attaining sexual maturity, the age structure and date of collection influence the comparisons. Most samples are similar in adult size (Fig. 3), but both sexes from Quepos and males from Escuintla are significantly larger. Respectively, these are the southern- and northernmost populations of *A. cupreus* sampled. Sexual difference in size is least in samples from San José and Cartago.

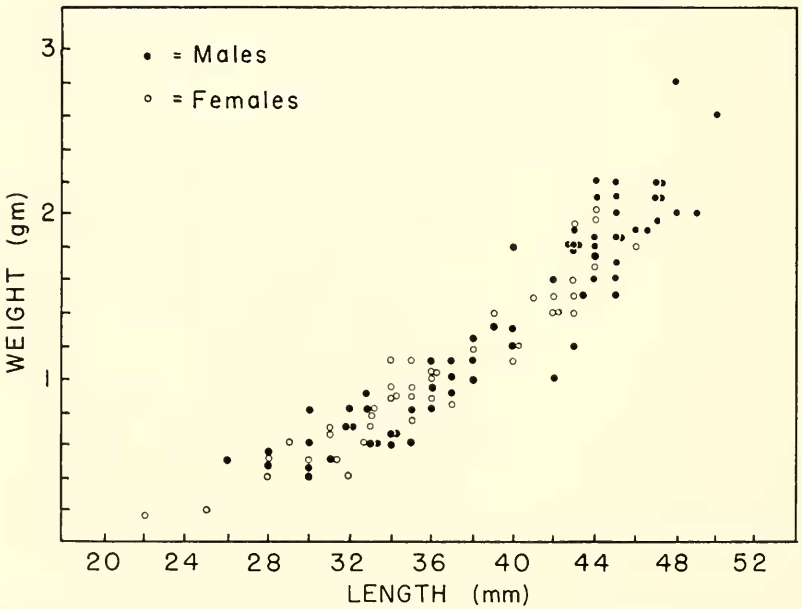

FIG. 2. The relationship between weight and snout-vent length in *Anolis cupreus* collected at San José, San José Province, Costa Rica, February 1970.

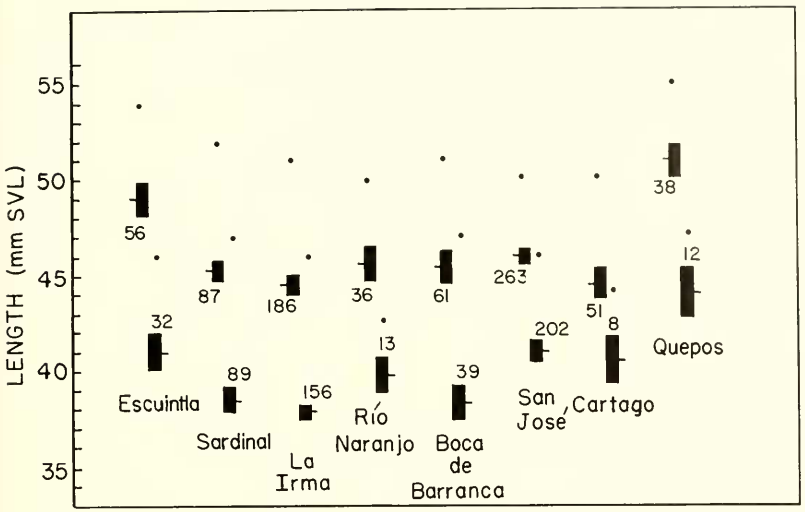

FIG. 3. Snout-vent lengths in adult *Anolis cupreus*, 35 mm or more in females (lower series of figures), 40 mm or more in males (upper series) from eight localities in Guatemala and Costa Rica. Dots indicate maximum lengths; horizontal lines represent means; bars show two standard errors on each side of the means; numbers are sample sizes.

Tail length.—Intact tails are proportionately longer in adults than in young. At Sardinal, Guanacaste Province, Costa Rica, the ratio of tail length to snout-vent length in 203 adults having snout-vent lengths of 40 mm or more is 1.60-2.00 (mean 1.77). Twenty hatchlings (probably in their first month of life) from the same locality have snout-vent lengths of 20 mm or less; the ratio of tail length to snout-vent length is 1.42-1.84 (mean 1.57). Adult males have relatively longer tails than females. Sexual dimorphism in tail length is less, if it exists at all, in hatchlings. In the adult series from Sardinal, the average ratio of tail length to snout-vent length is 1.80 in 112 males and 1.74 in 91 females. The series from the northern (Escuintla) and southern (Quepos) ends of the range have relatively long tails; whereas those from San José on the Meseta Central of Costa Rica are somewhat intermediate, and those from the lowlands of western Costa Rica (Sardinal, La Irma, Boca de Barranca) have relatively short tails (Table 1). The high ratio in females from Escuintla, slightly exceeding the male ratio, probably is an artifact of the small sample size.

Hind Limb.—No geographic variation could be demonstrated in our samples. In 77 per cent of 159 specimens, the fourth toe of the adpressed hind limb lies at a level between the anterior and

TABLE 1.—Comparisons of Various Populations of *Anolis cupreus*.
(Numbers in Parentheses = Sample Sizes)

	Escuintla	Playa del Coco	Sardinal	Taboga	Tilarán	La Irma	Río Naranjo	Boca de Barranca	Turrúcares	San José	Cartago	Quepos
Ratio of Tail Length to Snout-vent Length (Per cent)												
Males	(40)	—	(112)	—	—	(77)	—	(43)	—	(88)	—	(38)
Mean	186.5	—	180.0	—	—	178.8	—	180.2	—	184.4	—	186.9
Range	158-208	—	160-198	—	—	150-193	—	160-198	—	154-214	—	162-205
Females	(28)	—	(91)	—	—	(37)	—	(29)	—	(65)	—	(15)
Mean	186.8	—	173.9	—	—	174.8	—	175.3	—	177.1	—	179.4
Range	171-204	—	157-201	—	—	153-195	—	154-194	—	158-200	—	162-194
Scales around Midbody												
Males	(20)	(9)	—	(6)	(8)	(18)	(19)	—	(12)	(7)	(14)	(28)
Mean	134.0	132.4	—	135.8	119.5	115.1	122.0	—	116.8	114.4	106.8	136.4
Range	112-152	120-140	—	127-147	112-129	101-130	115-141	—	107-128	108-120	100-115	127-150
Females	(10)	(1)	—	(2)	(2)	(10)	(6)	—	(11)	(13)	(8)	(4)
Mean	120.0	120.0	—	125.0	123.5	112.4	118.8	—	110.6	110.6	102.1	127.7
Range	98-140	—	—	125	118-130	99-120	115-123	—	97-123	104-119	94-108	125-133
Digital Lamellae												
Mean	(20)	(11)	—	(8)	(8)	(24)	(25)	—	(23)	(22)	(23)	(32)

Both Sexes	8.70	8.45	----	8.25	7.63	8.46	9.60	----	8.92	8.65	8.83	9.30
Males	9.00	8.50	----	8.28	7.71	8.65	9.68	----	8.92	8.77	9.21	9.60
Females	8.40	8.00	----	8.00	7.00	8.20	9.33	----	8.90	8.44	8.22	8.44
Mode												
Males	9	9	----	9	8	9	10	----	9	9	9	10
Females	8	8	----	8	7	8-9	9	----	9	8	9	8
				Contact of Supraoculars with Supraorbital Semicircles (Per cent)								
	(40)	(10)	----	(8)	(10)	(28)	(25)	----	(23)	(20)	(22)	(32)
	38	30	----	25	63	64	64	----	59	75	73	39
				Frequency of Occurrence of Pattern Types in Females (Per cent)								
	(33)	----	(52)	----	----	(16)	(12)	----	(21)	(46)	(10)	(6)
Stripe	9.1	----	0.0	----	----	12.5	16.6	----	33.3	35.8	50.0	33.3
Diamonds	18.7	----	0.0	----	----	18.7	8.3	----	33.3	23.9	10.0	33.3
Chevrons	39.4	----	67.0	----	----	18.7	8.3	----	16.7	17.4	0.0	16.7
Nondescript	33.3	----	33.0	----	----	50.0	66.6	----	16.7	23.9	40.0	16.7

posterior corners of the eye; in 21 per cent it lies between the anterior edge of the ear and the eye, and in two per cent it lies slightly anterior to the eye. In six samples the hind limb is proportionately longer in males than in females, but in three samples the opposite is true.

Dewlap area.—The area of the extended dewlap was determined for live adult males (40 mm or more in snout-vent length) according to the method described by Echelle, Echelle and Fitch (1971). There is extensive overlap among the various populations in the ratio between the area of the dewlap and snout-vent length. The most divergent regression line is that for the sample from Escuintla in which the color pattern of the dewlap is also distinctive (Fig. 4).

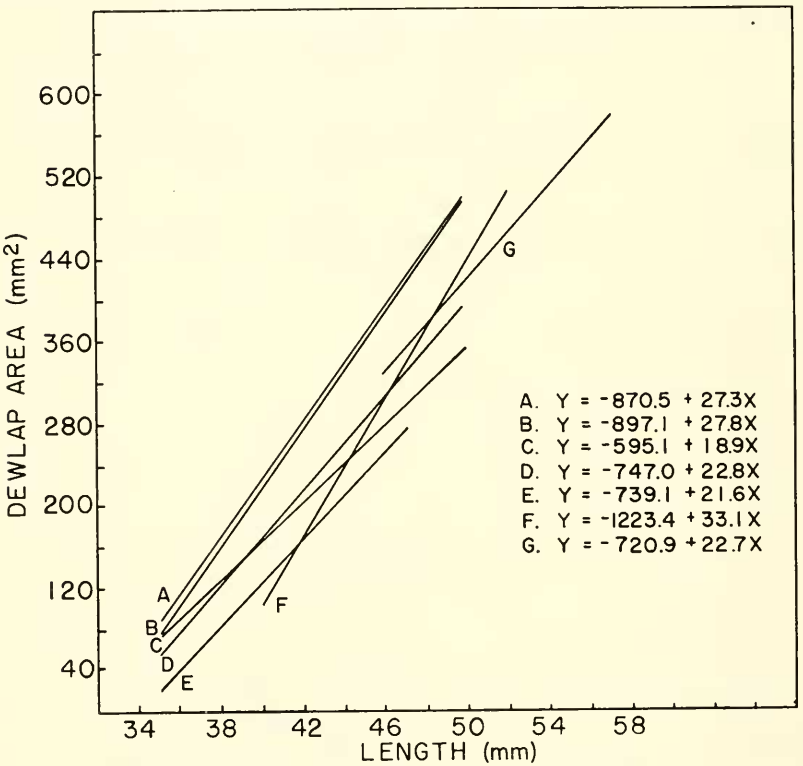

FIG. 4. Dewlap area on one side versus snout-vent length in adult males of *Anolis cupreus* from A. Río Naranjo; B. Turrúcares; C. San José; D. Cartago; E. Sardinal; F. Escuintla; G. Quepos.

Scale rows.—The number of scale rows around the middle of the body was a major character used by Williams and Smith (1966) to separate *A. cupreus* and *A. hoffmanni;* the latter authors stated that

six "*hoffmanni*" had 91 to 120 rows and eight "*cupreus*" had 134 to 145. The character is subject to much individual variation. Also there is an average difference between the sexes in number of scales (Table 1), a fact that apparently has not been noted previously. Because the dewlap is exceptionally large in male *A. cupreus*, extending slightly past mid-body, it probably affects the scale count. The scales of the dewlap and those of the belly and dorsum are relatively coarse, and variation in counts results partly from the granular scales of the sides being in irregular rows, making consistent counts difficult.

Anolis cupreus from the northern and southern ends of the range and from most other localities in the Pacific lowlands have relatively high numbers of scales around the body. The series from Turrúcares at an intermediate elevation (639 m) has lower numbers than most of the lowland series, and those from San José (1172 m) and Cartago (1435 m) have progressively lower numbers (Table 1). There is little or no overlap between the series from Cartago and those from the lowlands.

The type of *Anolis hoffmanni* had "approximately 92" scales around midbody (Williams and Smith, 1966), fewer than in any of the 211 specimens we counted. Williams and Smith also stated that counts of 91 [the type?], 108, 111, 114, 120, and 120 were obtained from specimens of *hoffmanni*. The lowest counts that we obtained (minimum 94) were in the series from Cartago; therefore, it seems most likely that the type of *A. hoffmanni* came from the Meseta Central, and perhaps, from the vicinity of Cartago.

Supraorbital semicircles.—In all specimens examined, the supraorbital semicircles are separated from the interparietal plate by small scales. Two scales occur more often (59%) than three (32%), and three more often than four (9%). In the small series from Tilarán and Río Naranjo the trend is reversed with three scales occurring more often than two. In all specimens examined, the supraorbital semicircles are separated by small scales that are variable in size, shape, and number. In each series the modal number is two (78% of total) with one (14%) and three (8%) occurring less frequently. No geographic variation is evident in this character.

Separation of supposed *Anolis hoffmanni* from *A. cupreus* by Williams and Smith (1966) depended largely on whether the large supraoculars were in contact with the supraorbital semicircles *(hoffmanni)* or separated from them in whole or in part by small intercalated scales *(cupreus)*. We examined this character in specimens from various localities; none of the populations is entirely

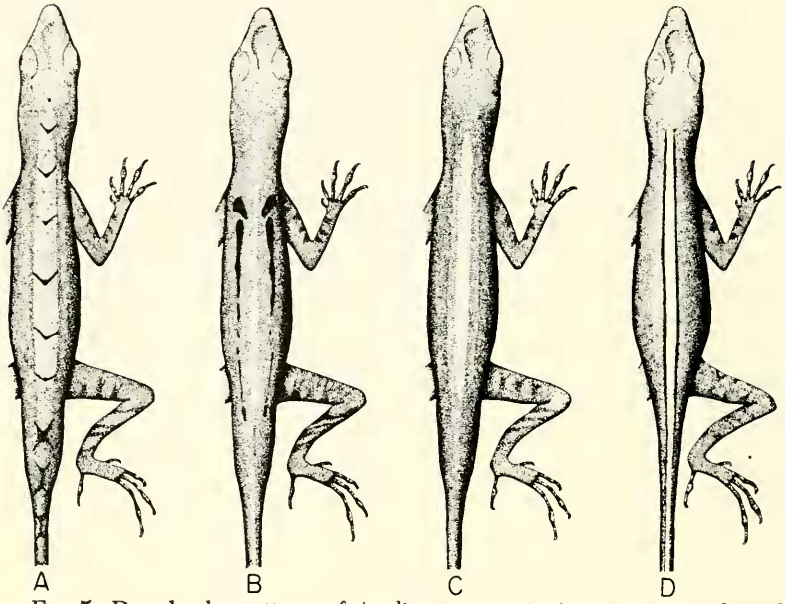

FIG. 5. Dorsal color patterns of *Anolis cupreus:* A. *A. c. cupreus* male with chevron pattern; B. *A. c. spilomelas* male with black shoulder patch and broken dorsolateral stripes; C. *A. c. hoffmanni* male with broad dull whitish middorsal stripe; D. *A. c. spilomelas* female with orange middorsal stripe edged with black. × 1.2.

"*hoffmanni*-like" (Table 1). Anoles from the Meseta Central (San José and Cartago) most commonly have the scales in contact, and samples from the Pacific lowlands most frequently have small intercalated scales. Samples from intermediate altitudes at Tilarán and Turrúcares are intermediate in character. The series from La Irma and Río Naranjo were unlike the other lowland samples in having more individuals which resemble upland populations with the supraoculars and semicircles in contact.

Digital lamellae.—The numbers of widened lamellar pads on the fourth toe vary as follows: 9 in 46.5%, 8 in 27.8%, 10 in 17.6%, 11 in 2.2%, 12 and 6 each in 0.6%. The number of lamellae is slightly higher in males than in females and possibly the character varies geographically (Table 1).

Coloration.—The color pattern of adult males is much less variable than that of females. There are three main pattern types with many intermediates or combinations: 1) White dorsum—a broad, poorly defined, dirty white middorsal area (Fig. 5C) edged with black or with tan tinged with ochre, which merges with the darker flanks. This pattern is most prevalent in populations on the Meseta Central (San José and Cartago) and is uncommon in lowland populations. Ordinarily it is not seen in juveniles, which have a chevron or nondescript pattern like adults of the Pacific lowlands.

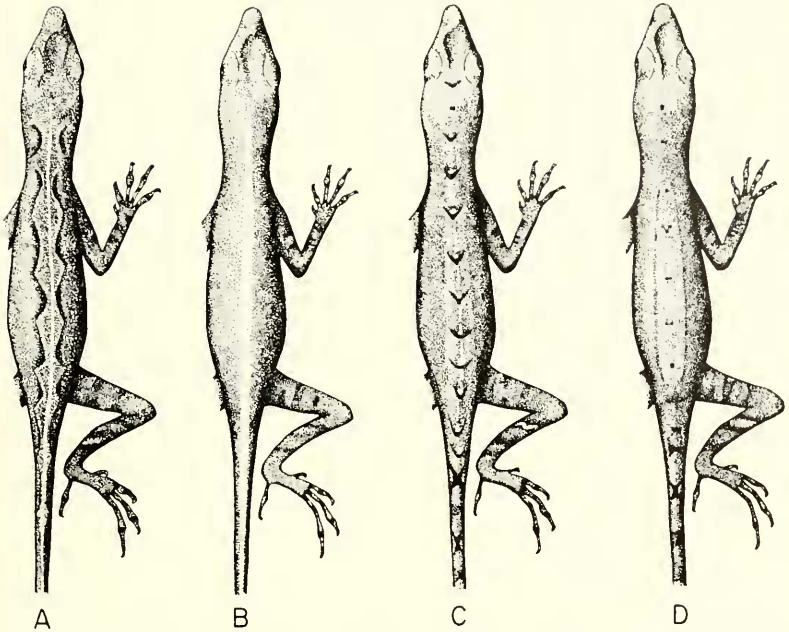

FIG. 6. Dorsal color patterns of female *Anolis cupreus:* A. *A. c. hoffmanni* with striped and diamond pattern; B. *A. c. hoffmanni* with broad, cream-colored dorsal stripe; C. *A. c. cupreus* with dorsal chevrons; D. *A. c. cupreus* with nondescript pattern. × 1.2.

2) Chevron markings—a series of middorsal transverse black marks that are usually chevron-shaped (Fig. 5A). Typically there are four or five chevrons on the body and two or three on the proximal part of the tail. In some individuals the markings are reduced to dots and the middorsal area bearing the dots is slightly paler than the sides. If the middorsal area is not set off as a pale band and if the chevrons are lacking, the pattern is referred to as "nondescript." The nondescript (sometimes nearly uniform drab brown) and chevron patterns are the common patterns in the Pacific lowlands. 3) Black-sided—heavy black pigmentation dorsolaterally, especially anteriorly (Fig. 5B). A black shoulder spot is prominent in some specimens. Variation includes a continuous but irregular streak, or a series of irregular spots and streaks on each side. The dorsal area between the black marks has chevrons or is nondescript. Although the tendency to have heavy pigmentation is most evident in the samples from Quepos, some individuals were found to be pale colored.

Like many other anoles, *Anolis cupreus* is characterized by pattern polymorphism in the females. At one locality as many as three distinctive patterns may be present among females. The frequency of occurrence of the different patterns varies from one

area to another, and a pattern that is common at one place may be absent at another. In one type of pattern there is a pale longitudinal middorsal stripe (Fig. 6B). The stripe varies in width from narrow to broad, and in color from creamy white to tan or bright orange; the margins of the stripe are darkened or boldly outlined in black. A second type of pattern consists of a longitudinal series of diamond shaped middorsal marks (Fig. 6A); usually the marks overlap, so that the posterior corner of one merges with the anterior part of the next. The markings are usually dark brown, but may be outlined by pale edges, and may enclose paler areas. The half of a diamond on one side of the midline may be displaced backward or forward from the other half so that the diamond markings are asymmetrical. Many individuals combine the diamond pattern with a pale middorsal stripe; in others the diamonds are not associated with such a stripe. A third type of pattern (Fig. 6C) lacks longitudinal lines and diamond markings but may have a series of middorsal black chevrons typical of some males. There are various degrees of intermediacy among the three types of patterns. Also there is some capacity for color change. Depending on temperature, illumination, and degree of excitation, there is darkening or lightening of general color, and markings that are well defined at one time may become faint at another. However, one type of pattern does not change to another. For the purposes of comparison, females lacking a dorsal stripe, diamond markings, and chevrons are termed "nondescript." The dorsum may be almost uniform brown, or have dark spots, dots, or flecks, usually middorsally. The flanks may bear tan or yellowish dots, or flecks.

At every locality where samples were obtained, the female pattern was highly variable (Table 1). At Cartago and San José on the Meseta Central the commonest type of pattern is the dorsal stripe (Figs. 6A and 6B); it occurs in one-third of the females from Quepos and Turrúcares. Farther north relatively few individuals are striped. Most females from Sardinal and La Irma have chevrons (Fig. 6C) or a nondescript pattern (Fig. 6D).

According to Williams and Smith (1966), an important difference between *A. cupreus* and *A. hoffmanni* is the dorsal color which is dark brown in *cupreus* and pale brown in *hoffmanni*. We suspect that this merely reflects individual variation; every population that we observed in the field was composed of some dark and light individuals with others being intermediate.

The dewlap is rudimentary and barely distensible in female *A. cupreus*. In all those from Guatemala, Guanacaste (Sardinal and La Irma) and Río Naranjo, the throat, or dewlap region, is plain

white, whereas in those females from Quepos it is white mottled with gray. Females from the Meseta Central are distinctive in having a trace of the pinkish orange like that which occurs on the male dewlap. Only two of 39 females from San José and one of 12 from Cartago have plain white throats that lack pinkish or orange. Specimens from Turrúcares are intermediate; only four of 21 have any color on the throat, and in each of these four the color is fainter than in most San José and Cartago specimens.

In general, characters of the dewlap are useful only when the living or freshly killed lizards are available. The dewlap cannot be spread in specimens preserved with it collapsed; moreover, on preservation, the colors become dull and nondescript. In male *Anolis cupreus* the dewlap is bicolor; the inner part is darker and sharply set off from the paler outer portion. In anoles from near Escuintla, and El Salto in Guatemala, the dark inner area is approximately half as large as that of Costa Rican specimens.

Almost every individul of *Anolis cupreus* has dusky bands on the arms, thighs, shanks, fingers and toes. Usually the bands are obscure, and they vary according to stage of molt and temperature. In our Guatemalan samples the bands seem to be more sharply defined on the digits than in the other samples.

RELATIONSHIPS

Our study focused on intraspecific variation, but various other species of anoles were observed in the field and/or examined in the laboratory. These observations, plus data from the literature, permitted us to form opinions regarding interspecific relationships. According to Etheridge (1960), *Anolis cupreus* belongs to the *chrysolepis* series of the Beta division of the genus *Anolis*. The *chrysolepis* series can be divided into several natural groups; many of the species are strikingly different from *A. cupreus*.

Anolis cupreus is the dominant anole on the Pacific versant of Central America from southeastern Guatemala to central Costa Rica. None of the numerous sympatric species seems to be closely related to it. *Anolis townsendi*, of Cocos Island (a remote Pacific island located almost midway between Costa Rica and the Galapagos) is remarkably like *cupreus* in size, most scale characters, and the stereotyped pattern of its aggressive display (see Carpenter, 1965). Possibly *A. townsendi* is a derivative of a *cupreus*-like ancestor which reached the island by rafting (Echelle, Echelle, and Fitch, 1971). Another close relative may be *Anolis cuprinus* Smith, as yet known only from the type locality near Zanatepec, Oaxaca,

México. It differs in having a unicolor dewlap that is smaller (reaching only to midthorax), and in having broad, V-shaped bands across the body. Stuart (1955:16) suggested that *Anolis dollfusianus* in Guatemala is a near relative of *A. cupreus*. This species seems to replace *cupreus* in the western two-thirds of Guatemala on the Pacific versant. Sympatric populations of the two species have not been recorded, but Stuart (1955:17) stated that *A. dollfusianus* occurs ". . . from about the level of Escuintla westward . . ." and we found *A. cupreus* to be abundant in the Escuintla area. *Anolis dollfusianus* differs from *cupreus* in smaller size (snout-vent length to 45 mm in 54 adults from near Retalhuleu), in having a smaller, yellowish dewlap, and in more rugose head shields. Its habits resemble those of *cupreus*, but the species is more slender and agile, similar in superficial appearance to *A. limifrons* of the Caribbean versant.

TAXONOMY

On the basis of our findings, *Anolis cupreus* is redescribed below; four subspecies, one named herein, are recognized.

Anolis cupreus Hallowell

Anolis cupreus Hallowell, 1860, Proc. Acad. Nat. Sci. Philadelphia, 1860:481.

Description.—Snout-vent length 35-57 mm in adults (males 40-57, mean 46; females 35-50, mean 40); brownish; scales on top of head large, rugose; ventral scales rhomboidal, imbricate, keeled, rounded posteriorly, much larger than dorsals; four median rows of dorsals larger than others; dorsal scales smallest about midlaterally, granular, in oblique and irregular rows; six or seven supralabials; seven or eight infralabials; two elongate supraciliaries; supraoculars keeled, in contact with supraorbital semicircles or separated by small intercalated scales, left and right sides often differing in this respect; six or seven rows of loreals; supraorbital semicircles usually separated from each other by one or two rows of scales; occipital nearly twice size of ear opening, separated from supraorbital semicircles on each side by two or three scales; caudal scales large, hexagonal, heavily keeled; most limb scales larger than those of body; some enlarged scales on dorsum of upper arm, anterior surfaces of forearm and thigh, and ventral surface of tibia; adpressed hind limb extending to region of eye; adpressed forelimb extending to region between eye and nostril; intact tail of adults 1.5-2.1 times snout-vent length (usually 1.8-1.9 in males and 1.7-1.8 in females); 6-12 (usually 8 or 9) lamellar pads on penultimate phalanx of fourth toe; dorsum nearly uniform pale or

dark brown, or variously marked with whitish, yellow, tan or orange, middorsal stripe edged with black or not, or with a series of middorsal black marks, usually chevron-shaped; black shoulder spots and black spots or streaks in dorsolateral area occasionally present; belly dull white with dusky suffusion; limbs somewhat paler than body; dusky bands, sometimes faint, on limbs and digits; dewlap of male large, rounded, extending from chin to midbelly or slightly beyond, bicolor, with dark amber-orange inner portion and pinkish rose outer portion.

Range.—Anolis cupreus inhabits Central America on, or near, the Pacific Coast (sea level to 1435 m) from southeastern Guatemala to Quepos in Costa Rica; it extends into the Caribbean versant, at least in the vicinities of Lago de Managua, Lago de Nicaragua, and Cartago in Costa Rica, but is confined to seasonally dry climates.

Anolis cupreus cupreus Hallowell

Anolis cupreus Hallowell, 1860. Proc. Acad. Nat. Sci. Philadelphia, 12:481.

Types.—None designated in original description; Stuart (1968: 62) listed 14 syntypes as follows: U.S. National Museum 12211 (11), Museum of Comparative Zoology 17631-32, and University of Illinois Museum of Natural History 40733, all from Nicaragua.

Diagnosis.—1) Small (average 45 mm snout-vent in adult males, 38 mm in adult females); 2) usually nondescript brown, lacking well defined pattern or with series of chevron-like middorsal marks in both sexes; 3) throat white in female; 4) average number of scales around mid-body more than 130 in males and more than 120 in females; 5) supraorbital semicircles in contact with supraoculars more often than not; 6) average ratio of tail length to snout-vent length approximately 1.80 in males and 1.75 in females.

The nominate subspecies differs from *A. c. hoffmanni* in having more scales around mid-body, white instead of pinkish or orange throat in female, and lower frequency of females having middorsal stripe and diamond pattern. The dark basal area of dewlap is approximately twice as large as in *A. c. macrophallus* and banding of the toes is less distinct. *Anolis c. cupreus* is smaller than *A. c. macrophallus* and *A. c. spilomelas;* it differs from the latter subspecies in the low frequency of males having black dorsolateral markings.

Range.—Anolis cupreus cupreus occurs in the Pacific lowlands from the northern part of Puntarenas Province through Guanacaste Province in Costa Rica, and northwest in Nicaragua to at least Managua, and probably to Honduras; it occurs in the Caribbean

versant on the west shore of Lago de Nicaragua (Sapóa), on Isla Ometepe, and on the south shore of Lago de Managua (Sabana Grande). We have not seen live material from Nicaragua but assume that the anoles there are similar to those from adjacent Guanacaste; in preservative they appear to be.

Anolis cupreus hoffmanni Peters
New combination

Anolis hoffmanni Peters, 1862, Monatsb. Akad. Wiss. Berlin, 1862:142.

Holotype.—Zoological Museum of Humboldt University, Berlin, 4690 from "Costa Rica" collected by C. Hoffmann. The type locality is hereby restricted to Cartago, Cartago Province, Costa Rica, because only in that area have anoles been found approximating the low number of scales around mid-body of the type. Although Hoffmann's itinerary has not been documented, the descriptions of his herpetological collection (Peters 1859, 1863) suggest that he must have travelled widely on the Atlantic and Pacific lowlands and in the Meseta Central.

Diagnosis.—1) Small (average 45 mm snout-vent in adult males, 40 mm in adult females); 2) adult males usually with broad, pale gray or brown middorsal band; females often with narrow, sharply defined middorsal stripe and/or a series of diamond shaped marks; 3) females with faint suffusion of pinkish or orange in throat area; 4) fewer than 120 scales around mid-body; 5) supraorbital semicircles usually in contact with supraoculars; 6) ratio of tail length to snout-vent approximately 1.84 in males and 1.77 in females.

This subspecies differs from other subspecies of *Anolis cupreus* in having fewer scales around mid-body, greater frequency of contact between supraoculars and supraorbital semicircles, and pink or orange on throat of female. *Anolis cupreus hoffmanni* is distinguished from *A. c. macrophallus* and *A. c. spilomelas* by its smaller average and maximum size.

Range.—*Anolis cupreus hoffmanni* occurs on the Meseta Central in Costa Rica, from approximately 600 m to 1435 m; chiefly on the Pacific versant but in the Cartago area on the Caribbean versant there is a population separated from the main population by the continental divide.

Anolis cupreus macrophallus Werner
New combination

Anolis macrophallus Werner, 1917, Jahrb. Hamburg Miss. Anat., 34:31.

Holotype.—Formerly in Zoologisches Museum, Hamburg, but

destroyed in World War II (*fide* Stuart, 1955:15), from San José, Department of Escuintla, Guatemala.

Diagnosis.—1) Large (average 49 mm snout-vent in adult males, 41 mm in adult females); 2) nondescript in both sexes, usually brown with no well defined pattern or with series of chevron-like middorsal marks; 3) throat white in female whereas dewlap in male is pinkish or rose with a darker, orange basal area which is relatively small, only about half as large as in the other subspecies; 4) average number of scales around mid-body 134 in males and 120 in females; 5) supraorbital semicircles in contact with supraoculars in approximately one-third of specimens; 6) ratio of tail length to snout-vent approximately 1.87 in both sexes.

This subspecies differs from *Anolis cupreus spilomelas* in its smaller size and lack of black dorsolateral marks. *Anolis c. macrophallus* differs from *A. c. cupreus* and *A. c. hoffmanni* in its larger size and is uniquely distinguished by the relatively small, darkened (orange) area at base of male dewlap.

Range.—*Anolis cupreus macrophallus* occurs in southeastern Guatemala in lowlands and at intermediate elevations (to 1400 m), from San José, Escuintla and Palin across the southern part of El Salvador. Mertens (1952:41) listed and described 21 specimens from nine localities in El Salvador.

Presumably *Anolis cupreus* has a continuous range along the Pacific Coast of Central America, at least from San José, Guatemala to Quepos, Costa Rica, but records are lacking from the 300 km interval between Cuscatlán, El Salvador and Managua, Nicaragua. The gap separating known populations of *A. c. macrophallus* and *A. c. cupreus* includes the Honduran coast at the Gulf of Fonseca and the areas adjacent to it in El Salvador on the west and Nicaragua on the south and east.

Anolis cupreus spilomelas new subspecies

Holotype.—KU 140593 from Quepos, Puntarenas Province, Costa Rica, obtained by H. S. Fitch, on 23-24 February, 1970.

Paratypes.—KU 140594-605, 140607-19, California Academy of Sciences 133124-6, Museum of Comparative Zoology 129776-8, same data as holotype.

Diagnosis.—1) Large (average 51 mm snout-vent in adult males, 44 mm in adult females); 2) heavy black dorsolateral spots, streaks or lines; female pattern variable with pale middorsal stripe or diamond shaped markings or chevrons, or nondescript; 3) throat white, mottled with gray in female; 4) average number of scales around mid-body 136 in males, 128 in females; 5) supraorbital semicircles separated from supraoculars in majority (61 per cent) of specimens;

6) ratio of tail length to snout-vent approximately 1.87 in males and 1.79 in females.

Description of holotype.—Snout-vent length 51 mm, tail 63 mm, head 9 mm long, snout 6 mm wide; adpressed hind limb extending forward to middle of eye; 133 scales around mid-body; 8 supralabials on each side, seventh beneath middle of eye; 7 postrostrals; 9 scales between nasals; 4 scales between frontal ridges at widest point; 2 scales between supraorbital semicircles; 3 scales between semicircles and occipital; occipital slightly larger than ear; 8 loreals on each side; 2 large superciliaries on each side; 8 canthals on left, 7 on right; 4 large suboculars left and right; scales on top of head strongly keeled; canthus rostralis strongly developed; 9 infralabials on each side, the 8th below middle of eye; 4 rows of enlarged middorsal scales on body; 9 lamellae on penultimate phalanx of fourth toe on each side; eye 1.5 times diameter of ear opening; a large black rounded shoulder spot on each side followed by black streaks that extend to mid-body.

Range.—Anolis cupreus spilomelas occurs on the coastal plain and adjacent foothills of northern Puntarenas Province in the Quepos-Parrita area of Costa Rica. Almost certainly the range is continuous with that of *A. c. cupreus* to the northwest, but material is lacking from a 77-km interval between Boca de Barranca, the southernmost station for *A. c. cupreus* and Parrita, the northernmost station for *A. c. spilomelas.*

Etymology.—The subspecific name *spilomelas* is from Greek, *spilos*—spot and *melas*—black, referring to the prominent black marks often present on the shoulder and dorsolateral region.

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RESUMEN

Anolis cupreus se encuentra distribuido en el sureste de Guatemala, extendiendose hacia el sureste especialmente en las tierras

bajas del Pacifico, hasta Costa Rica. Además, su distribución se extiende hacia el caribe en áreas relativamente áridas del Lago Nicaragua y en el centro de Costa Rica en los alrededores de Cartago. El tamaño del cuerpo, la proporción de cabeza y cola, el número de escamas alrededor del cuerpo, el diveño del saco gular, el color de la quihoda, el diseño dorsal del cuerpo, y detalles en la escamación de la cabeza varian geograficamente y están subjectos a mucha variación individual, con marcadas diferencias entre los sexos. El polimorfismo en el diseño de las manchas del cuerpo de las hembras es común. Varios autores han considerado a menudo *Anolis hoffmanni* Peters, como un sinónimo de *A. cupreus*, pero también autores contemporaneos los han catalogado como diferentes especies. Sin embargo, todas las características descritas para *Anolis hoffmanni* se encuentran presentes en las poblaciones de *A. cupreus*. Las cuales están muy bien desarrolladas en la población de la Meseta Central en Costa Rica. Consideramos que *Anolis cupreus hoffmanni* es una subespecie endémica de esta area, caracterizada por el tamaño relativamente pequeño, por el diseño en lineas, y por el color rosado o anaranjado de la quijada de las hembras. Otras subespecies son: *A. c. spilomelas* del área Quepos-Parrita en Costa Rica, distinquiéndose por su tamaño grande, y por las marcas dorsolaterales negras; *A. c. cupreus* que aparece desde Puntarenas extendiendose al noroeste de Costa Rica, hasta el occidente de Nicaragua, distinquiéndose por su tamaño pequeño y con diseños indifinibles o con manchas angulares mediodorsales; y *A. c. macrophallus* de El Salvador y sureste de Guatemala, el cual se distingue por una mancha oscura relativamente pequeña en la base del saco gular del macho.

SPECIMENS EXAMINED

Anolis cupreus cupreus. COSTA RICA, *Guanacaste:* Finca Bosco, KU 40743; Finca Taboga, KU 129253; 5 km W Liberia, 100 m, KU 66866; La Irma, Río Congo, KU 125703-8, 140565-92; Las Cañas, KU 40747-51; 16 km SSE Las Cañas, KU 66865; Ojotal, 2 km SW El Coco, KU 66860-61; "Pacific slope," KU 40744-46; Playa del Coco, KU 129245-52; Río Bebedero 2.5 km S Bebedero, KU 66862-64; 4-5 km ENE Tilarán, KU 40752-63 and 40995; 7 mi NE Tilarán, KU 86555. *Puntarenas:* 6 mi E Esparta, KU 56032; Marbella Hotel, KU 40739-40 and 40742.

NICARAGUA, *Managua:* 2 mi N Sabana Grande, 50 m, KU 85637. *Rivas:* Isla Ometepe, 40 m, 3 km N Moyogalpa, KU 85641; Río Javillo, 3 km N and 4 km W Sapóa, 40 m KU 85368-40.

Anolis cupreus hoffmanni. COSTA RICA, *Alajuela:* 5-10 km E Sarchi, KU 40737-38; Turrúcares, KU 140620-63. *Cartago:* Cartago, KU 140664-738. *San José:* Las Pavas, 4.8 km W San José, KU 125681-89; San José, KU 40741, 125613-80, 125690-92, 125817-22, 140739-69.

Anolis cupreus macrophallus. GUATEMALA, *Escuintla:* El Salto, near

Escuintla, KU 140862-75; 0.5 mi S Escuintla, KU 140770-832; 4.6 mi S Escuintla, KU 140833-46, 140848, 140850-61.

Anolis cupreus spilomelas. COSTA RICA, *Puntarenas:* Quepos, CAS 133124-6, KU 125693-94, 140594-605, 140607-19, MCZ 129776-8; 2.4 km E Quepos, KU 125695; 6.4 km NNW Quepos, KU 125696; 1.6 km N Quepos, KU 125701-02; 2.4 km N Río Cañas, KU 125697-700.

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